PROC. BIOL. SOC. WASH.
102(4), 1989, pp. 924–932

AN UNUSUAL SPECIES OF THE *BALANUS AMPHITRITE* DARWIN COMPLEX (CIRRIPEDIA, BALANIDAE) FROM THE ANCESTRAL COLORADO RIVER DELTA IN WESTERN ARIZONA AND SOUTHEASTERN CALIFORNIA

Victor A. Zullo and Anna V. Buising

Abstract.—Shells and opercular plates of *Balanus canabus,* new species, form shell hashes in the upper Cenozoic Bouse Formation of western Arizona and southeastern California. The thin, columnar shells and morphologically variable opercular plates indicate growth of large, crowded colonies in low salinity waters. The vesicular sheath and the overall morphology of the opercular and compartmental plates are characteristic of the genus *Fistulobalanus* Zullo, but the lack of multiple rows of parietal tubes precludes assignment to this genus. *Balanus canabus* is not clearly related to any extant eastern Pacific species, but does resemble the western Pacific species *Fistulobalanus albicostatus* (Pilsbry) and *F. kondakovi* (Tarasov & Zevina) and the Atlantic and Indian Ocean species *F. pallidus* (Darwin).

Barnacle hashes in the Bouse Formation of western Arizona and southeastern California (Fig. 1) are formed by the shells of a single species of balanid barnacle. The hashes consist of partially crushed, extremely thin-walled, columnar to tulipiform shells with intact opercular pyramids, together with disarticulated compartmental and opercular plates (Fig. 4e). The new species is remarkable in the thinness of its plates and, particularly, in the unusual growth modifications of its scuta and terga. The carinal margins of the terga and the upper occludent margins of the scuta are reflexed inward through secondary growth, creating an expanded compartment at the apex of the opercular pyramid.

The tubiferous shell wall with numerous transverse septa, the tubiferous basis, the narrow radii with finely denticulate sutural edges, and the well developed scutal adductor ridge, serve to identify this species with the diverse and widespread *Balanus amphitrite* Darwin complex (see Henry & McLaughlin 1975). Although the overall morphology of the opercular plates and the vesicular sheath of the new species are characteristic of the genus *Fistulobalanus* Zullo, the lack of multiple rows of parietal tubes precludes assignment to this genus.

Stratigraphy and Paleoenvironments of the Bouse Formation

The outcrop belt of the Mio-Pliocene Bouse Formation includes more than 3000 km^2 of discontinuous exposure in western Arizona and southeastern California (Fig. 1). Strata now assigned to the Bouse Formation were recognized early in the twentieth century (e.g., Blanchard 1913), but were not formally named until later regional work by Metzger (1968). The Bouse Formation was recently re-examined by Buising (1988) on whose study the following discussion of stratigraphy and sedimentology is based.

Strata of the Bouse Formation are interpreted as documenting transgression of what is now the lower Colorado River trough by waters of the proto-Gulf of California, a tec-

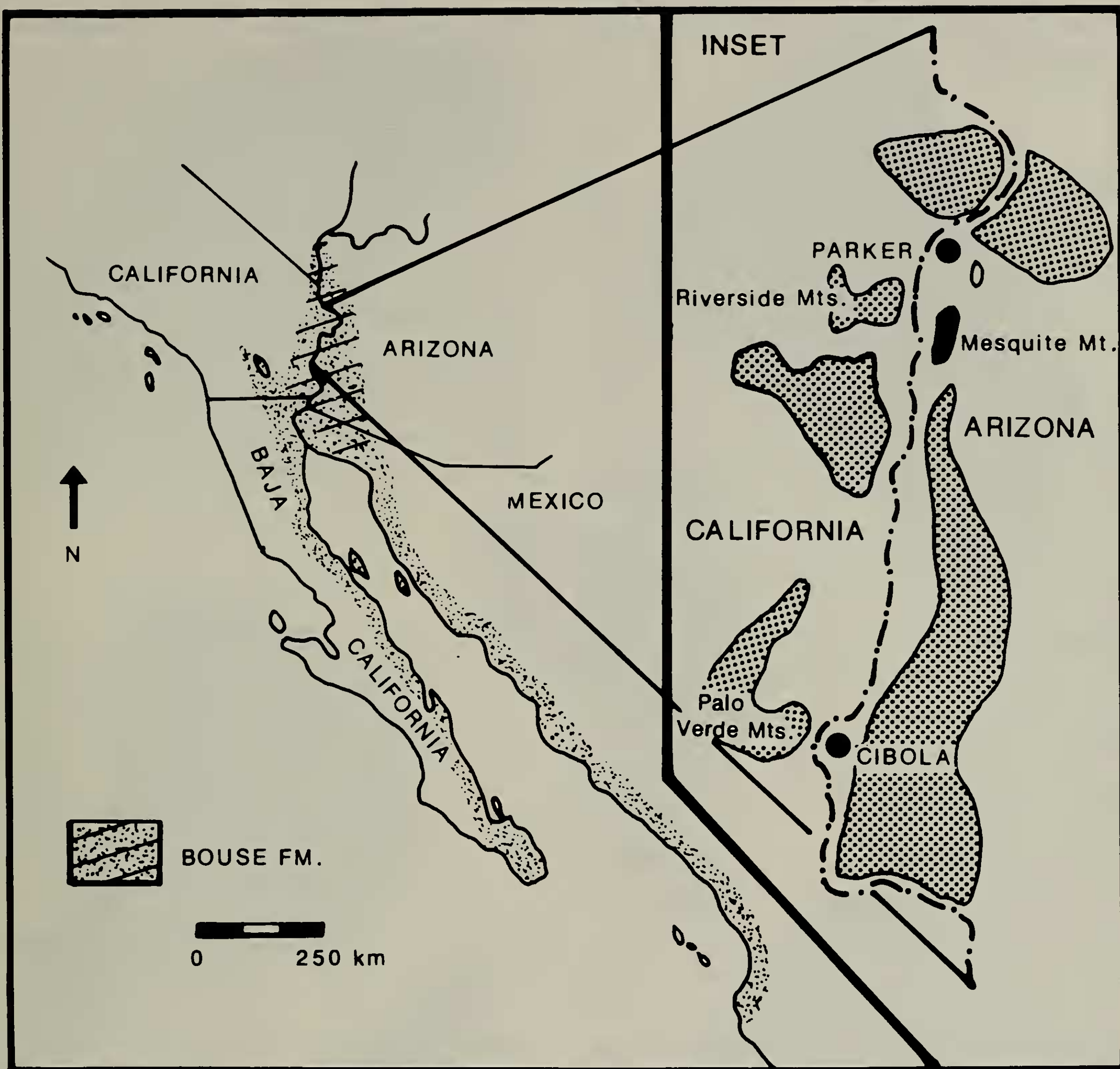

Fig. 1. Distribution of Bouse Formation (cross-hatched) in relation to inferred extent of proto-Gulf outcrop belt (stippled). Inset shows mountain ranges (stippled) of the lower Colorado River region and location of Mesquite Mountain, type locality of *B. canabus* (after Buising 1988).

tonically complex marine embayment that occupied the Gulf of California physiographic province prior to onset of modern spreading- and transform-generated subsidence in that region (Fig. 1). Basal transgressive carbonate of the Bouse Formation overlies pre-Bouse fanglomerate, reflecting inundation of an internally drained alluvial system during proto-Gulf subsidence. The basal carbonate is overlain by fine-grained terrigenous clastic strata recording the southward progradation of the ancestral Colorado River delta into the proto-Gulf. These deltaic facies interfinger laterally with a shoreline complex that includes algal tufa, clastic limestone and barnacle coquina, as well as coarse-grained, terrigenous clastic units derived from the erosion of local island and basin-margin highs. The Bouse Formation is overlain by, and interfingers with trough cross-bedded cobble conglomerates, informally called the Colorado River gravels, that are characterized by a clast assemblage derived from the Colorado Plateau, and are interpreted as recording arrival of the through-going Colorado fluvial channel in approximately its modern position. Although the age of the Bouse Formation remains problematic, recent reevaluation suggests that it was deposited between eight and four million years ago (Buising 1988).

Paleoecology

With the exception of channel lag occurrences, such as those at Mesquite Mountain, and of isolated occurrences in distributary channel siltstone, the barnacles are usually associated with coarse terrigenous clastic units and algal tufa that mark the shoreline of the proto-Gulf (Buising 1988). The proto-Gulf shoreline, which is preserved in essentially its original depositional configuration, was extremely rugged and rocky and, presumably, provided the principal substratum for the barnacles. However, barnacles were not found attached to rocks in the shoreline facies, and the only examples found in life position were attached to algal tufa at a shoreline locality northeast of the type channel lag deposits at Mesquite Mountain (Buising 1988).

The abundance of barnacles, and thinness and morphological variability of their plates, indicate rapid, seasonal growth in waters of lowered salinity. Low salinity waters are also suggested by algal tufa morphology and $^{87/86}$Sr values of tufa and barnacle shell samples (Buising 1988). The crowded, columnar to tulipiform growth habit suggests that hard substrata suitable for settlement were limited, and that vertical growth was a necessary prerequisite for competition under crowded conditions. In addition, some depositional environments of the Bouse Formation suggest that rapid vertical growth was essential to maintaining the individual above the terrigenous clastic detritus being deposited in the delta system.

It is likely that cyprid larvae were carried into the delta by the advancing salt wedge during the dry season, and settled in dense masses on every available hard substratum. Adult size was probably attained within a single year, as at least two size classes are recognized, appearing to represent separate yearly settlement. The parietes and scuta of the larger size class, which attained an average adult height of one cm, are overgrown by smaller individuals averaging about one-half cm in height. Although the limited use of calcium carbonate in the shell is indicative of growth in lowered salinities, neither size class shows any evidence of the shell corrosion common in such brackish water species as *Balanus eburneus* Gould and *Fistulobalanus pallidus* (Darwin). This is particularly interesting as the larger size class appears to have lived for more than a single year and, thus, long enough for corrosion to occur.

Systematics

Family Balanidae Leach, 1817
(Newman & Ross 1976)
Subfamily Balaninae Leach 1817
(Newman 1980)
Genus *Balanus* Da Costa, 1778
Balanus canabus, new species
Figs. 2–4

Holotype.—Partially crushed opercular pyramid, USNM 423910.

Type locality.—Bouse Formation, west flank of Mesquite Mountain, La Paz County, Arizona.

Diagnosis.—Shell thin, cylindric to tulipiform, with smooth parietes; radii narrow, with steeply sloping summits and denticulate sutural edges; alae extremely broad, with horizontal summits and denticulate sutural edges; sheath vesicular; parietal tubes rectangular, in single row. Scutum very thin, extremely convex or medially sulcate, much taller than broad; external longitudinal striae very fine or absent; articular ridge about one-half length of tergal margin; adductor ridge short, well separated from articular ridge; depressor muscle pit shallow and triangular or absent. Tergum very thin, broad, externally convex, with convex carinal margin and narrow, sometimes deep, spur furrow broadening toward spur; upper carinal margin reflexed inward to form broad in-

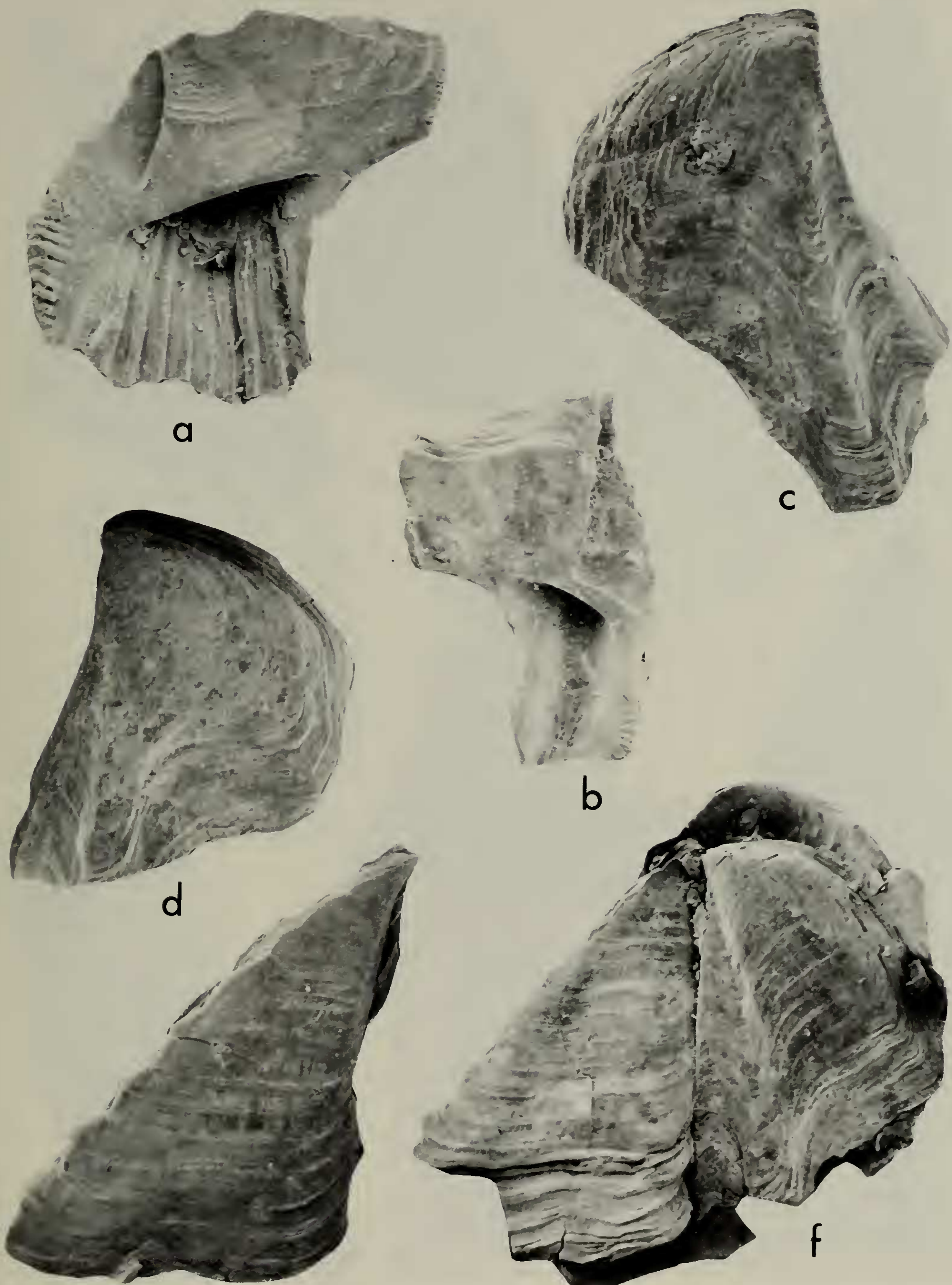

Fig. 2. *Balanus canabus*: a, Interior of lateral plate, paratype USNM 423920, ×27; b, Interior of carinolateral plate, paratype USNM 423921, ×11; c, Exterior of tergum, paratype USNM 423922, ×11; d, Exterior of tergum (lacking spur), paratype USNM 423923, ×12; e, Exterior of scutum, paratype USNM 423924, ×12; f, Articulated opercular pyramid, holotype USNM 423910, ×12.

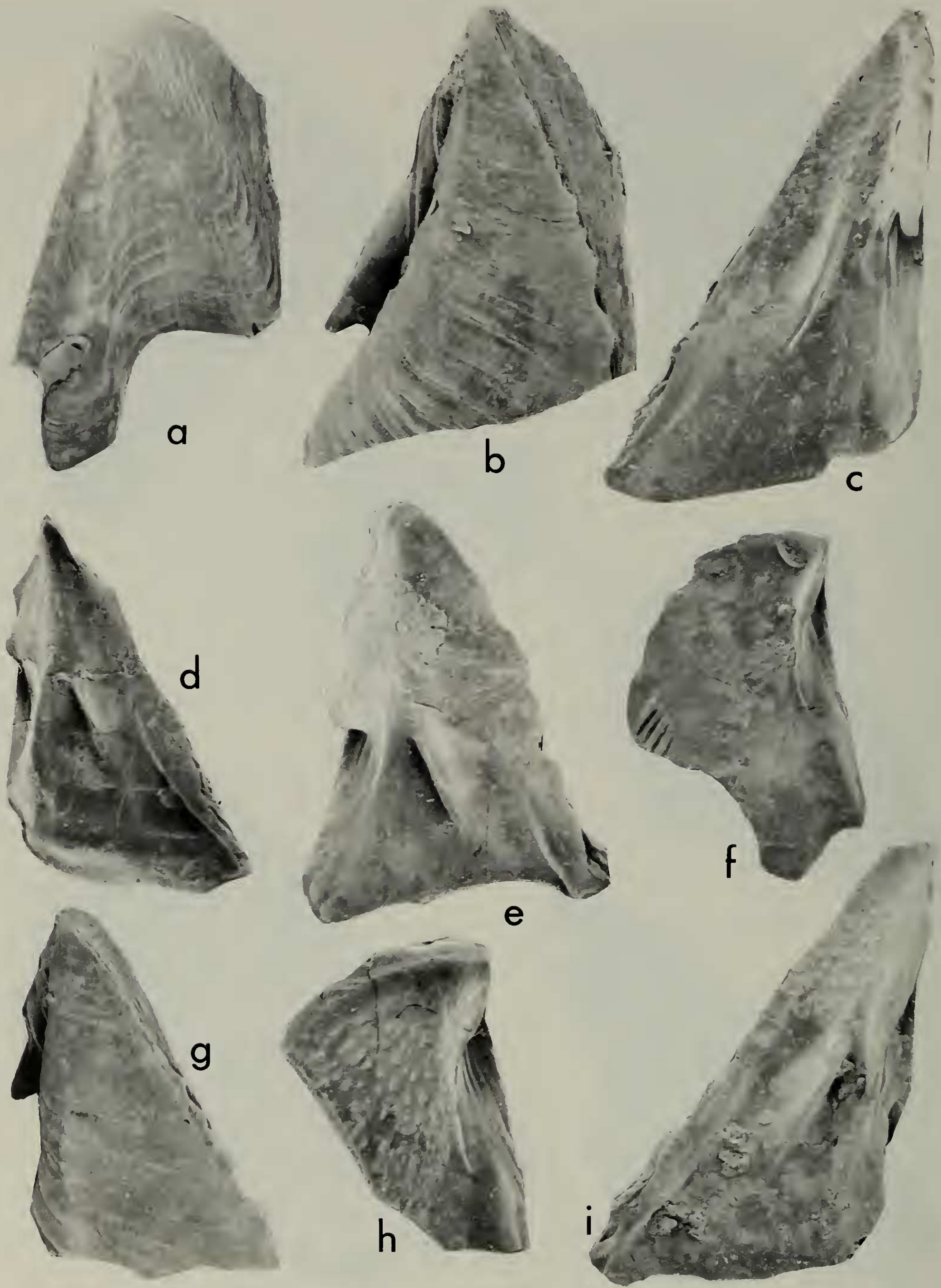

Fig. 3. Opercular plates of *Balanus canabus*: a, Exterior of tergum, paratype USNM 423911, ×12; b, Exterior of apical half of scutum showing secondary extension of occludent margin (on right side), paratype USNM 423912, ×18; c, Interior of scutum, paratype USNM 423913, ×12; d–e, Interiors of scuta, paratypes USNM 423914 through 423915, ×16; f, Interior of tergum, paratype USNM 423916, ×12; g, exterior of scutum, paratype USNM 423917, ×12; h, Interior of tergum (lacking spur) showing apical compartment, paratype USNM 423918, ×12; i, Interior of scutum, paratype USNM 423919, ×14.

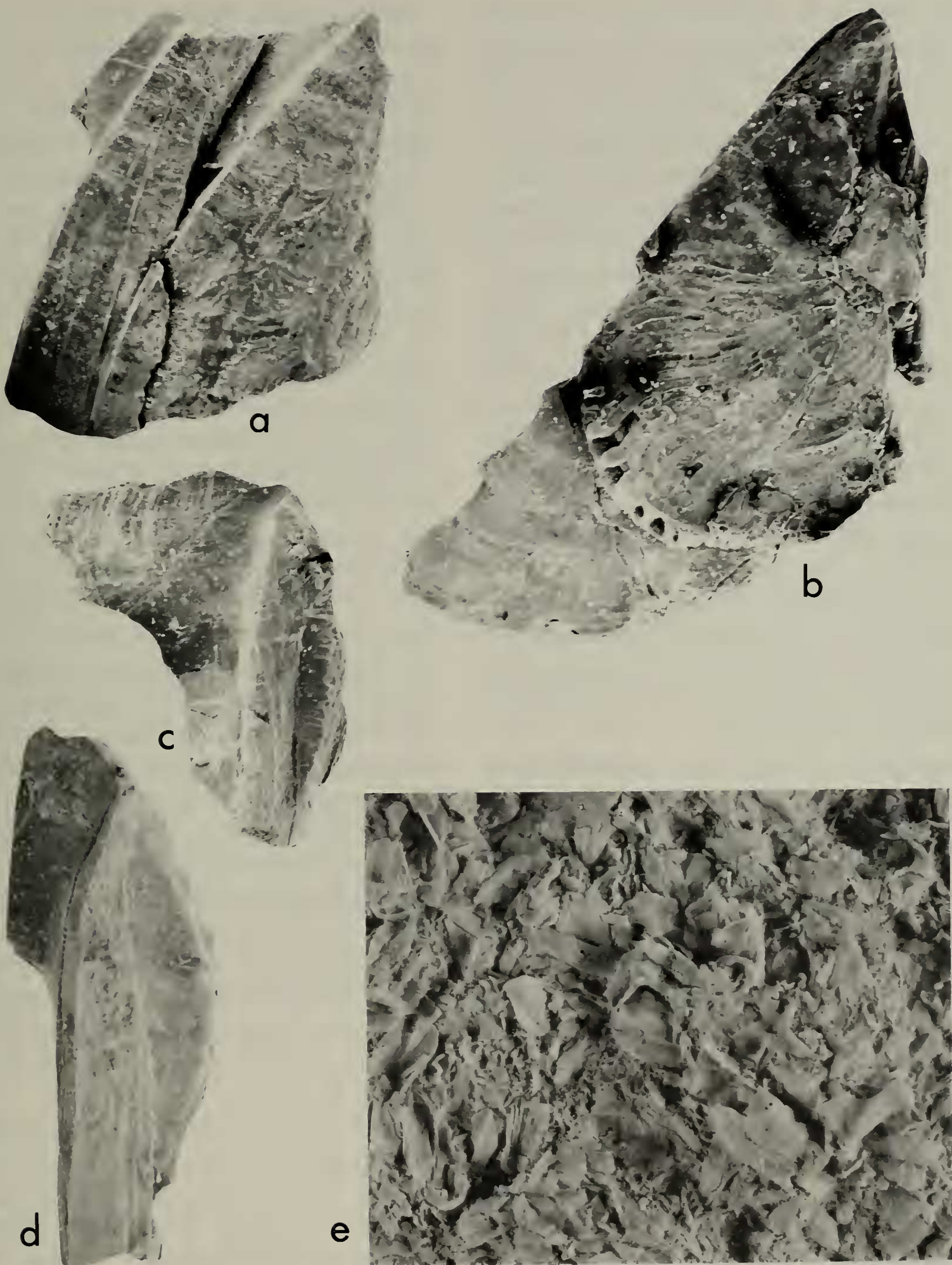

Fig. 4. *Balanus canabus*: a, Articulated lateral and carinolateral plates, paratype USNM 423925, ×25; b, Basis of second generation individual attached to scutum, paratype USNM 423926, ×19; c, Exterior of carinolateral showing distal extension of ala, paratype USNM 423927, ×11; d, Carinolateral of cylindric individual, paratype USNM 423928, ×11; e, Barnacle hash from channel lag deposit of type locality, paratype lot USNM 423929, ×1.5.

ternal shelf; spur slightly longer than wide, basally subtruncate; distance from basiscutal angle to spur less than or equal to spur width; basal margin straight to concave on both sides of spur, not deeply excavated.

Material.—Twenty-seven shells with or without opercular plates; over 1000 disarticulated compartmental plates; 77 whole or partial scuta; 65 whole or partial terga.

Disposition of types.—Holotype USNM 423910, paratypes USNM 423911 through 423928, and paratype lot USNM 423929 are deposited in the collection of the Department of Paleobiology, National Museum of Natural History, Washington, D.C.

Geologic and geographic range.—Late Cenozoic (probably latest Miocene or Pliocene), Bouse Formation, southeastern California and western Arizona.

Etymology.—The specific name is derived from the Greek *kanabos,* meaning "a mere skeleton," and refers to the extremely thin shell of this species.

Description.—Shell thin, cylindric to tulipiform in adults, high conic in juveniles, with slightly toothed orifice and smooth parietes; a few specimens show traces of broad, longitudinal color stripes on parietes; radii narrow, not sunken, transversely striate, with steeply sloping summits (70°) and thin, finely crenate, sutural edges; alae very broad, composed of proximal and distal segments separated by incised diagonal line and change in growth pattern; horizontal to convex summits of alae formed by distal segments; alar sutural edges finely crenate; sheath about one-third length of compartmental plate, vesicular, without vesicles in furrow below dependent lower margin; internal parietal ribs prominent, regularly spaced, flat-topped, extending from base to sheath, finely crenate basally; longitudinal parietal tubes large, rectangular, in single row, crossed by numerous, closely spaced, transverse septa; basis calcareous, thin in center and thickening appreciably toward margin, with fine radial tubes bearing few transverse septa.

Scutum thin, narrow, with basal margin two-thirds to three-fourths length of tergal margin; exterior either flat with median longitudinal sulcus or broadly convex; apex often twisted slightly toward tergum; exterior ornamented by broadly spaced major growth ridges forming denticles on occludent margin and numerous, fine, minor growth ridges between major ridges; exterior growth ridges usually crossed by extremely fine longitudinal striae in central part of plate; tergal margin straight to slightly concave, broadly reflected from 45° to 60° from plane of plate; occludent margin convex, sharply inflected in upper half; inflected area of occludent margin often enlarged by secondary growth in apical region; basal margin straight to slightly sinuous; articular ridge prominent, usually about one-half length of tergal margin, forming a broad, flat shelf in upper half, becoming narrow and sharp in lower half, and ending in sharp, downturned hook, partially reflected over deep, narrow, articular furrow; adductor ridge sharp, erect, highest adjacent to adductor muscle pit, variable in length, but usually short, centrally located, and well removed from articular ridge; adductor muscle pit shallow, small, round to oval; a shallow, triangular pit often present on tergal side of adductor ridge; depressor muscle pit either moderately large, shallow and triangular or absent; interior of apical half of scutum rugose.

Tergum thin, convex, broad, with basal margin one-half to two-thirds length of plate; carinal margin convex, usually protuberant apically, sharply inflected in apical half forming internal apical chamber; scutal margin straight to concave, sharply inflected to form flat shelf; basal margin not deeply embayed, straight to concave on either side of spur; exterior ornamented by closely spaced major, and a few interspersed minor, growth ridges; broad area along carinal margin marked by sharply upturned growth lines; carinal side of exterior bearing fine radial striae partially reflecting position of internal depressor muscle crests; spur furrow narrow in apical half, widening toward spur, often very deep; sides of spur furrow not marked by incised lines and not infolded; spur with nearly parallel sides and subtruncate base, placed between one-half its width and distance equal to its width from basiscutal angle, moderately long, about two-ninths length of plate, and narrow, less than one-third width of basal margin; articular ridge nearly erect, high, thin, concave on scutal side, little more than one-half length of scutal margin, and continuous with inflected part of carinal margin forming apical chamber; articular furrow broad, moderately deep; depressor muscle crests short, well developed, closely spaced, usually five in number; interior or tergum markedly rugose in apical half.

Discussion.—Aside from the marked thinness of the compartmental and opercular plates, the features that set the new species apart from other members of the *Balanus amphitrite* complex are those apparently associated with the broadening of the orifice with continued vertical growth under crowded conditions. Development of the tulipiform shell is accomplished through secondary distal growth of the alae rather than widening of the radii. In fact, the steeply sloping radius is in contact with the paries of the adjacent compartment only in the basal third of the shell wall. The opercular pyramid, which occupies most of the orifice, accommodates the increase in orifice diameter through secondary horizontal growth on either side of the aperture formed by the occludent margin of the scutum and the carinal margin of the tergum. This horizontal growth produces a chamber in the apex of the opercular pyramid which is particularly apparent on the interior of the tergum. A similar chamber is seen in terga of the extant western Pacific species *Fistulobalanus albicostatus* (Pilsbry) and *F. kondakovi* (Tarasov & Zevina). The growth form and resulting morphology of *B. canabus* appear to be related both to competition for living space under crowded conditions in an area of limited substrata, and to maintenance of the individual above the sediment that was being deposited in the delta environment.

Although *B. canabus* shares many morphological features with fossil and extant species of *Fistulobalanus,* it lacks multiple rows of parietal tubes in the shell wall and, therefore, cannot be included in the genus. The similarity of the new species to *Fistulobalanus* is striking, however. All of the extant species of the genus are found in brackish waters (Henry & McLaughlin 1975; the habitats of *F. abeli* (Lamy & André) and of *F. patelliformis* (Bruguière) are unknown). Some specimens of *F. pallidus* and *F. kondakovi* lack subsidiary parietal tube rows, and these species often occur in crowded, thin-walled, cylindric masses in brackish water environments (Stubbings 1963; Henry & McLaughlin 1975). The morphology of the opercular and compartmental plates of *B. canabus* is typical of *Fistulobalanus,* especially of *F. pallidus, F. albicostatus* and *F. kondakovi,* and bears less resemblance to species of *Balanus.* The absence of subsidiary parietal tubes may be related to the crowded, columnar growth habit and the conservative use of calcium carbonate in shell construction.

It is possible that *B. canabus* was derived from a *Fistulobalanus* ancestor. The genus extends back to the middle Miocene in the North Atlantic basin (Zullo 1984), and is known from the Pleistocene of Japan (Yamaguchi 1980). However, the two extant species of *Fistulobalanus* known from the eastern Pacific, *F. dentivarians* (Henry) and *F. suturalis* (Henry), bear less resemblance to *Balanus canabus* than do the previously mentioned western Pacific and Atlantic Ocean species.

Among the species of the *B. amphitrite* complex with a single row of parietal tubes, only the extant western Atlantic species *B. eburneus* and *B. subalbidus* Henry possess a vesicular sheath. Like the species of *Fistulobalanus,* both are inhabitants of brackish waters. *Balanus eburneus* differs in having radii with broader, gently sloping summits; prominent, deeply incised external radial striae on the scutum; a scutal adductor ridge that is almost confluent with the articular ridge; and a tergum with a spur fasciole and a markedly concave and usually deeply embayed basal margin on the carinal side of the spur. *Balanus subalbidus* differs in having a broader scutum with the adductor and articular ridges nearly confluent, and a tergum with a spur fasciole and a broader spur.

Locality Descriptions

The type lot of *B. canabus* was obtained from the fine-grained, terrigenous-clastic, deltaic facies of the Bouse Formation on the west flank of Mesquite Mountain, La Paz County, Arizona. At this locality, transported barnacles and barnacle plates occur as a lag deposit in a northerly-trending channel approximately 5 m wide and slightly less than 1 m deep. The channel, filled with green mud, is located at the western terminus of a pink siltstone bed with pervasive, westward-migrating, meter-high, trough cross-beds. The entire complex is interpreted as representing progressive westward migration of a tidally-influenced distributary channel, followed by channel abandonment and infilling by green hypoxic mud (Buising 1988).

Other specimens of *B. canabus* examined for this study were collected in 1961 by Blakemore E. Thomas, San Diego State University, from Bouse Formation outcrops on the north end of the Riverside Mountains, Riverside County, and the Palo Verde Mountains, Imperial County, California.

Acknowledgments

We thank the people and council of the Colorado River Indian Tribes for allowing access to tribal lands in the Mesquite Mountain area for mapping and sampling purposes. Special thanks are extended to Charles Lamb, Weldon Johnson, Curtis Martin and the Colorado River Indian Tribes Museum.

Literature Cited

Blanchard, R. C. 1913. The geology of the western Buckskin Mountains, Yuma County, Arizona.—Columbia University Contributions of the Geology Department 26:1–80.

Buising, A. V. 1988. Deposition and tectonic evolution of the northern proto-Gulf of California and lower Colorado River, as documented in the Mio-Pliocene Bouse Formation and bracketing units, southeastern California and western Arizona. Unpublished Ph.D. dissertation, University of California at Santa Barbara, 196 pp.

Henry, D. P., & P. A. McLaughlin. 1975. The barnacles of the *Balanus amphitrite* complex (Cirripedia, Thoracica).—Zoologische Verhandelingen 141, 254 pp.

Metzger, D. G. 1968. The Bouse Formation (Pliocene) of the Parker-Blythe-Cibola area, Arizona and California.—United States Geological Survey Professional Paper 600-D:D126–D136.

Stubbings, H. G. 1963. Cirripedia of the tropical south Atlantic coast of Africa.—Expédition Océanographique Belge dan las Eaux Côtières Africaines de l'Atlantique Sud (1948–1949), Institut Royal des Sciences Naturelles de Belgique, Résultats Scientifiques 3(10), 39 pp.

Yamaguchi, T. 1980. A new species belonging to the *Balanus amphitrite* Darwin group (Cirripedia, Balanomorpha) from the late Pleistocene of Japan.—Journal of Paleontology 54:1084–1101.

Zullo, V. A. 1984. New genera and species of balanoid barnacles from the Oligocene and Miocene of North Carolina.—Journal of Paleontology 58:1312–1338.

(VAZ) Department of Earth Sciences, University of North Carolina at Wilmington, North Carolina 28403; (AVB) Department of Geological Sciences, California State University, Hayward, California 94542.